

Owens, I. P. & Bennett, P. M. (1994) Mortality costs of parental care and sexual dimorphism in birds. *Proc. Royal Soc. London B*. 257: 1–8.

Pietz, P. J. & Granfors, D. A. (2000) Identifying predators and fates of grassland passerine nests using miniature video cameras. *J. Wildlife Manage.* 64: 71–87.

Reif, V. & Tornberg, R. (2006) Using time-lapse digital video recording for a nesting study of birds of prey. *Eur. J. Wildlife Res.* 52: 251–258.

Rothstein, S. I. & Robinson, S. K. (1998) *Parasitic birds and their hosts: studies in coevolution*. New York: Oxford University Press.

Semel, B. & Sherman, P. W. (2001) Intraspecific parasitism and nest-site competition in wood ducks. *Anim. Behav.* 61: 787–803.

Shy, M. M. (1982) Interspecific feeding among birds: a review. *J. Field Orn.* 53: 370–393.

Aiwu JIANG, Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning, 530004, China. Email: aiwuu@163.com

Demeng JIANG, College of Forestry, Southwest Forestry University, Kunming, 650224, China and Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning, 530004, China. Email: jdm447268365@163.com

Eben GOODALE & Yuanguang WEN, Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning, China, 530004. Email: eben.goodale@outlook.com & wenyg@263.net

Fang ZHOU, College of Animal Science and Technology, Guangxi University, Nanning, 530004, China. Email: zhoufang768@126.com

What happens when the nuclear species is absent? Observations of mixed-species bird flocks in the Hiyare Forest Reserve, Galle, Sri Lanka

P. L. MEAURANGA M. PERERA, SARATH W. KOTAGAMA, EBEN GOODALE & H. S. KATHRIARACHCHI

Introduction

Mixed-species flocks play a prominent role in the social organisation of birds, especially in the tropics (Greenberg 2000, Sridhar *et al.* 2009) and it has long been observed that some ‘nuclear’ species play essential roles in the formation, maintenance and leadership of mixed-species flocks (Moynihan 1962, Goodale & Beauchamp 2010). Several authors have suggested that when nuclear species are absent, flocks may break up, and this might make flocking species vulnerable to human disturbance (Maldonado-Coelho & Marini 2004, Sridhar & Sankar 2008, Zhang *et al.* 2013). This could be a particularly interesting example of why non-trophic species interactions should be taken into consideration when devising strategies for conservation (Valiente-Banuet *et al.* 2015).

Here we report on flocks that persist in the absence of a typical nuclear species. In the lowlands of the wet zone of Sri Lanka, Orange-billed Babbler *Turdoides rufescens* demonstrates all the characteristics of a nuclear species: it is noisy and active, highly gregarious and leads most flocks (Kotagama & Goodale 2004, Jayarathna *et al.* 2013). A secondary nuclear species might be the Greater Racket-tailed Drongo *Dicrurus paradiseus lophorhinus*; this taxon—considered by some authorities to be an endemic monotypic species, the Sri Lanka Crested Drongo *Dicrurus lophorhinus*—makes loud alarm calls (Goodale & Kotagama 2005a) and is as attractive to other species as babblers in playback experiments (Goodale & Kotagama 2005b). However, it is not gregarious and does not facilitate the foraging of other birds, being a sallying species, and one that can also be aggressive and kleptoparasitic (Satischandra *et al.* 2007). At the Hiyare Forest Reserve study site there are no Orange-billed Babblers, but the Sri Lanka Crested Drongo is present.

Methodology

The study was made in the Hiyare Forest Reserve, Galle, a low altitude (about 350 m) rainforest patch in Southern province, Sri Lanka (6.667°N 80.283°E), about 16 km east of Galle (Figure 1A). We selected this site because it is similar in climate and vegetation to the Sinharaja Man and Biosphere Reserve, a long-term study site of mixed-species flocks (Kotagama & Goodale 2004), 70 km to the north-east, although the forests near Galle are more heavily fragmented. The reserve is small (about 240 ha), although it is close to the larger Kottawa-Kombala Forest Reserve; the forest at the site has been protected since 1919 because of the presence of a 20 ha reservoir, and thus is relatively mature. We made observations at three sites in

the forest (Figure 1B) that were located more than 200 m from each other. Flocks were sampled in October and November 2010 and February to May 2011, between 06h00 and 14h00. We made only one observation per site per day. As flocks reformed every morning and showed as much variation at one site as between sites, we have pooled the observations here.

Flocks were defined as birds of more than one species clearly moving together in a group, and were followed for an average of 15 minutes until we believed all individuals moving with the flock had been counted. All species seen at least once during the observation period were counted as flock participants and the highest number of individuals seen at any one time was recorded as the number of individuals of that species in the flock.

Results

We observed 28 flocks, which averaged five species (SD ± 3) and nine individuals (SD ± 5.6) per flock. The species observed were quite similar to the flocks observed by Kotagama & Goodale (2004) at Sinharaja, with eight of the ten species seen in more than 20% of the flocks in Hiyare (Table 1) also being seen in Sinharaja. Eleven other species not mentioned in Table 1 participated in fewer than 20% of the Hiyare flocks (less than six flocks): Common lora *Aegithina tiphia*, Golden-fronted Leafbird *Chloropsis aurifrons* and Tickell’s Blue Flycatcher *Niltava tickelliae jerdoni* in five flocks, Purple-rumped Sunbird *Nectarinia zeylonica zeylonica* in four flocks, Sri Lanka

Table 1. Species recorded in 28 mixed-species foraging flocks in the Hiyare Forest Reserve in 2010–2011. Diet/foraging technique: IS = insectivorous, sallying; IP = insectivorous, probing; IG = insectivorous, leaf-gleaning; F = frugivorous.

Species	Number of flocks	Average number per flock	Diet / technique
Sri Lanka Crested Drongo <i>Dicrurus lophorhinus</i>	14	1.7	IS
Dark-fronted Babbler <i>Rhopocichlo otriceps</i>	14	3.2	IG
Yellow-browed Bulbul <i>Acritillos indica</i>	13	1.7	IG, F
Malabar Trogon <i>Horpocetes fosciotus</i>	12	1.4	IS
Black-naped Monarch <i>Hypathymis azurea</i>	12	1.6	IS
Asian Paradise-flycatcher <i>Terpsiphane paradisi</i>	8	1.0	IS
Black-capped Bulbul <i>Pycnanatus melanicterus</i>	8	1.6	F, IG
Orange Minivet <i>Pericratus flammeus</i>	7	1.7	IG
Black Bulbul <i>Hypsipetes ganeeso</i>	6	1.8	F, IG
Lesser Sri Lanka Flameback <i>Dinopium psorodes</i>	6	1.2	IP

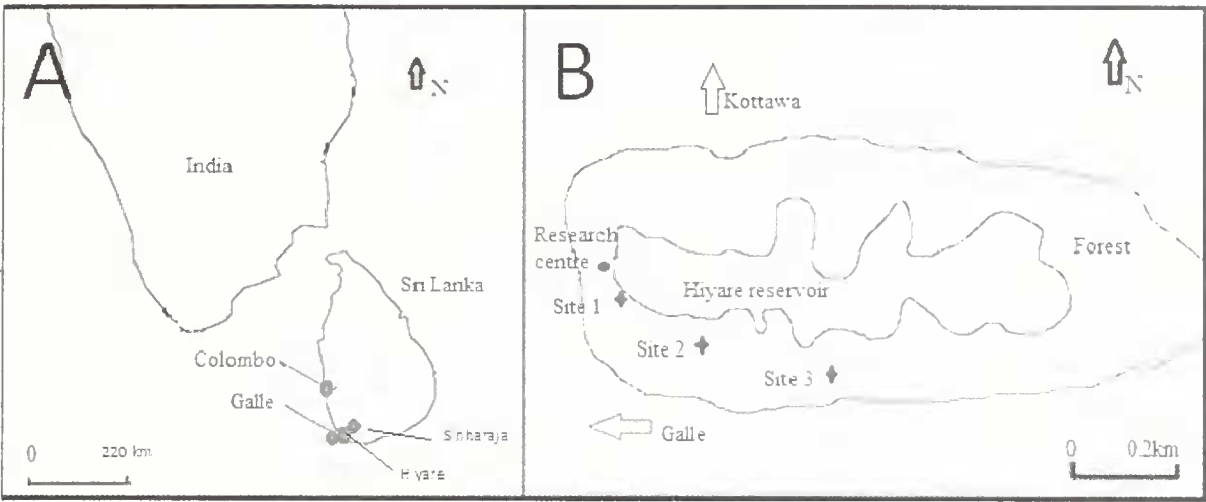


Figure 1A. Location of Hiyare Forest Reserve and Sinharaja Reserve relative to Galle.

Figure 1B. A schematic map of the site showing the three sampling locations.

Scimitar Babbler *Pomatorhinus melanurus*, Small Minivet *Pericrocotus cinnamomeus* and Sri Lanka Yellow-fronted Barbet *Megalaima flavifrons* in three flocks, and Brown-headed Barbet *Megalaima zeylanica*, Pale-billed Flowerpecker *Dicaeum erythrorhynchos ceylonense*, Sri Lanka Grey Hornbill *Ocyrceros gingalensis* and White-rumped Shama *Copsychus malabaricus leggei* in two flocks.

Discussion

Our observations show rather surprisingly that flocks similar to those described by Kotagama & Goodale (2004) exist in this small forest patch, but with a key difference: the absence in Hiyare of the Orange-billed Babbler, which is the most frequent, the most numerous and the leading species in Sinharaja. The experience of watching a flock in Hiyare is very different from Sinharaja, as the Hiyare flocks are very quiet, with Sri Lanka Crested Drongo and Yellow-browed Bulbul *Acritillas indica* only occasionally calling or singing. Flocks did not move very far, apparently moving round in circles, and we were not able to discern which species was leading them. No flock included more than two individuals of any one species, except for the Dark-fronted Babbler *Rhopocichla atriceps* that lives in small family groups of 3–4 individuals; these flocks are atypical for Asia, where flocks usually include very gregarious species (Goodale *et al.* 2009).

Similar observations of flocks without babblers have been made in other lowland forest fragments, including those near a Buddhist temple in Horana, Kalutara district, Western province (EG pers. obs.). During radio-tracked observations in Sinharaja, we found that drongo species sometimes dropped out of babbler-led flocks, but were found in small quiet flocks, especially with other sallying species such as monarchs, paradise-flycatchers and trogons. These flocks, without the activity of numerous leaf-gleaning species, might be expected to offer very different benefits, at least in foraging efficiency, compared with babbler-led flocks of the Sinharaja system. A detailed study of foraging rate and efficiency of Hiyare-like flocks, compared with the more typical flocks in which the Orange-billed Babbler is present, would be a useful future direction, enabling us to better understand the benefits that nuclear species give to other flock participants in mixed-species flocks.

References

Goodale, E. & Beauchamp, G. (2010) The relationship between leadership and gregariousness in mixed-species bird flocks. *J. Avian Biol.* 41: 99–103.
Goodale, E. & Kotagama, S. W. (2005a) Alarm calling in Sri Lankan mixed-species bird flocks. *Auk* 122: 108–120.
Goodale, E. & Kotagama, S. W. (2005b) Testing the roles of species in mixed-species bird flocks of a Sri Lankan rainforest. *J. Trop. Ecol.* 21: 669–676.
Goodale, E., Nizam, B. Z., Robin, V. V., Sridhar, H., Trivedi, P., Kotagama, S. W., Padmalal, U. K. G. K., Perera, R., Pramod, P. & Vijayan, L. (2009) Regional variation in the composition and structure of mixed-species bird flocks in the Western Ghats and Sri Lanka. *Curr. Sci. India* 97: 648–663.

Greenberg, R. (2000) Birds of many feathers: the formation and structure of mixed-species flocks of forest birds. Pp.521–558 in: S. Boinski & P. A. Garber, eds. *On the move: how and why animals travel in groups*. Chicago: University of Chicago Press.
Jayarathna, A., Kotagama, S. W. & Goodale, E. (2013) The seasonality of mixed-species bird flocks in a Sri Lankan rainforest in relation to the breeding of the nuclear species, Orange-billed Babbler *Turdoides rufescens*. *Forktail* 29: 138–139.
Kotagama, S. W. & Goodale, E. (2004) The composition and spatial organisation of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20: 63–70.
Maldonado-Coelho, M. & Marini, M. A. (2004) Mixed-species bird flocks from Brazilian Atlantic forest: the effects of forest fragmentation and seasonality on their size, richness and stability. *Biol. Conserv.* 116: 19–26.
Moynihan, M. (1962) The organization and probable evolution of some mixed-species flocks of Neotropical birds. *Smithson. Misc. Coll.* 143: 1–140.
Satischandra, S. H. K., Kudavidanage, E. P., Kotagama, S. W. & Goodale, E. (2007) The benefits of joining mixed-species flocks for a sentinel nuclear species, the Greater Racket-tailed Drongo *Dicrurus paradiseus*. *Forktail* 23: 145–148.
Sridhar, H., Beauchamp, G. & Shanker, K. (2009) Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* 78: 337–347.
Sridhar, H. & Sankar, K. (2008) Effects of habitat degradation on mixed-species bird flocks in Indian rain forests. *J. Trop. Ecol.* 24: 135–147.
Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M. & Jordano, P. (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29: 299–307.
Zhang Q., Han R. C., Zhang M., Huang Z. & Zou F. (2013) Linking vegetation structure and bird organization: response of mixed-species bird flocks to forest succession in subtropical China. *Biodivers. Conserv.* 22: 1965–1989.

P. L. Meauranga M. PERERA, Department of Plant Sciences, University of Colombo, Sri Lanka. Email: meauranga_perera@yahoo.com (corresponding author)

Sarath W. KOTAGAMA, Department of Zoology, University of Colombo, Sri Lanka. Email: fogsl@slt.lk

Eben GOODALE, College of Forestry, University of Guangxi, Nanning, Guangxi, China. Email: eben.goodale@outlook.com

H. S. KATHRIARACHCHI, Department of Plant Sciences, University of Colombo, Sri Lanka. Email: hashi@pts.cmb.ac.lk